

AMPHIBIA: ANURA: HYLIDAE

HYLA CINEREA

Catalogue of American Amphibians and Reptiles.

Redmer, M. and R.A. Brandon. 2003. *Hyla cinerea*.

***Hyla cinerea* (Schneider)**
Green Treefrog

Calamita cinereus Schneider 1799:174. Type locality, "Carolina," restricted to "Charleston, South Carolina" by Schmidt (1953). Type(s), unknown.

Calamita Carolinensis: Schneider 1799:174. Substitute name for *C. cinerea*, attributed erroneously to Pennant (1792).

Hyla lateralis Daudin 1800:21. Type locality, "environs de Charlestown [= Charleston]," South Carolina. Type(s), unknown.

Rana bilineata Shaw 1802:136. Type locality, "...warm and temperate parts of North America," restricted to "Charleston, South Carolina" by Schmidt 1953. Holotype, Catesby (1754) plate 71, one of the earliest available color illustrations (examined by authors).

Calamita lateralis: Merrem 1820:171. "Habitat in America septentrionalis."

Hyla viridis Holbrook 1840:4. Preoccupied by *Hyla viridis* Laurenti 1768 (= *H. arborea*).

Hyla semifasciata Hallowell 1857 ("1856"):307. Type locality, "Texas," restricted to "vicinity of Houston, Texas" by Schmidt (1953). Syntypes, Academy of Natural Sciences, Philadelphia (ANSP) 2024–2025 (Malnate 1971), adults, sexes undetermined, date of collection unknown, donated by "Dr. Heermann" (not examined by authors).

Hyla carolinensis: Günther 1859 ("1858"):105.

Hyla carolinensis semifasciata: Cope 1875:31. "...Texan district."

Hyla cinerea: Garman 1890:189.

Hyla cinerea Var. *cinerea*: Garman 1892:346.

Hyla cinerea Var. *semifasciata*: Garman 1892:346–347. "An example from Bluff Lake, Union county [Illinois], conforms more closely with Hallowell's variety *semifasciata* than with type forms of the species."

Hyla cinerea semifasciata: Rhoads 1895:397.

Hyla evittata Miller 1899:75. Type locality, "Four Mile Run, Alexandria [Fairfax] County, Virginia." Holotype, National Museum of Natural History (USNM) 26291, adult male (47 mm), collected 15 July 1899 by G.S. Miller and E.A. Preble (not examined by authors).

Hyla cinerea evittata: Dunn 1918:21.

• **CONTENT.** No subspecies currently are recognized, but see **Nomenclatural History.**

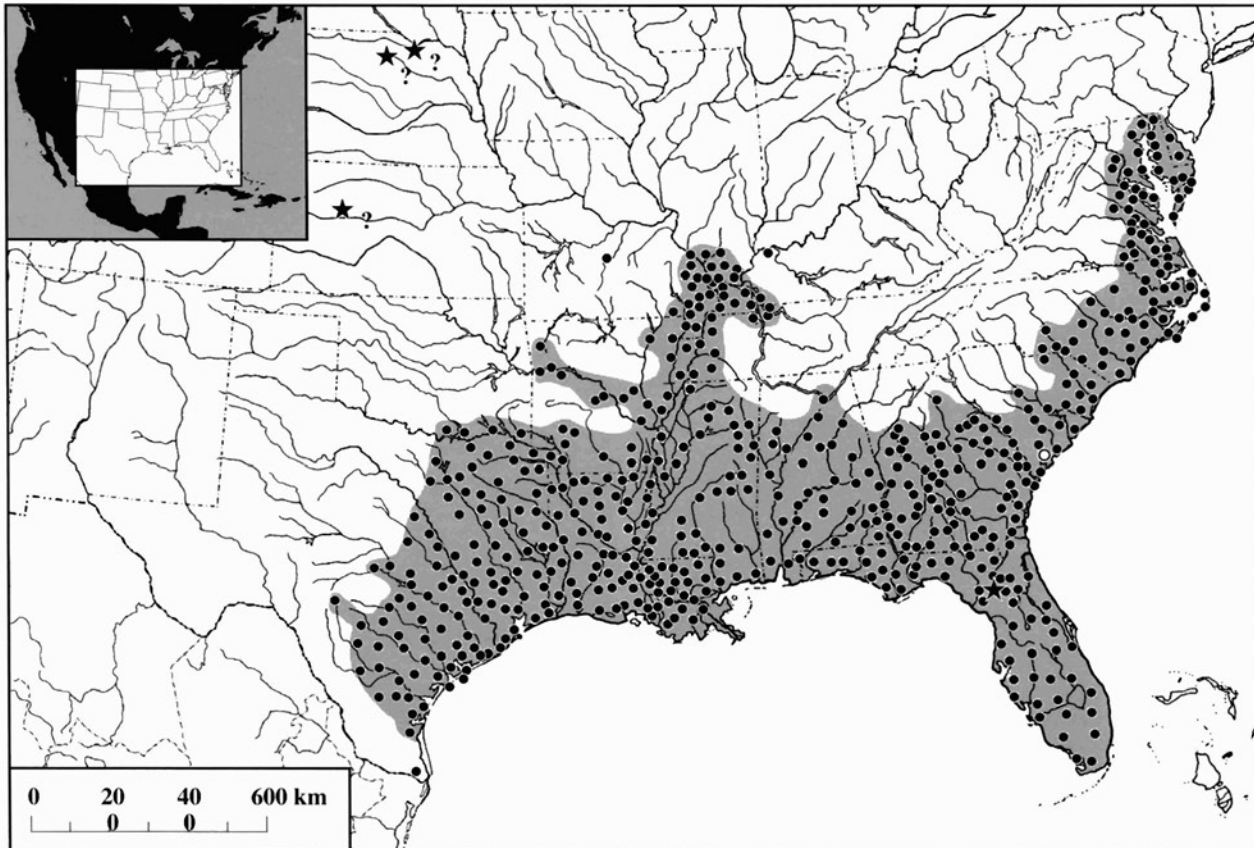


FIGURE 1. Adult male *Hyla cinerea* from Union County, Illinois (top) and calling male *H. cinerea* from Pulaski County, Illinois (photographs by M. Redmer).

• **DEFINITION.** *Hyla cinerea* is a wide-ranging, moderately large North American hylid frog. Adults range from 32–64 mm SVL (Conant and Collins 1998), with females averaging slightly larger than males. In life, the back and side skin is smooth, light to dark green, usually with a white or yellow (often bordered by black) lateral stripe extending along each side from the angles of the jaw to the thigh, and the back often has scattered white or yellow spots. In some populations, occasional individuals lack lateral stripes (see **Pertinent Literature** and **Nomenclatural History**). The granular ventral skin is white. Males have a single, external, subgular vocal sac, which when not inflated is mostly white or yellow in color, though its sides may be green during the breeding season. In preservative, adults quickly fade from



FIGURE 2. *Hyla cinerea* tadpole from Pope County, Illinois (photograph by M. Redmer).



MAP. Distribution of *Hyla cinerea*: the circle indicates the type locality, dots mark other localities. The star in Florida indicates a fossil record. Stars and question marks in Kansas and Nebraska indicate fossil records of "*Hyla cf. cinerea*." The introduced population in Puerto Rico is not illustrated.

green to ashen gray and light dorsolateral stripes (not visible in life) often appear over the subcutaneous insertions of lymph-sac septa. Several months after preservation, specimens usually appear mostly dark green or brownish in color. Folds of skin occur between the axillae and from above the tympana to the shoulders. The head is flat and the snout is pointed. Two transverse rows of vomerine teeth are present. Toe pads are large. One large palmar tubercle occurs at the base of the inner finger and numerous smaller ones on the hand. Tarsal folds, two metatarsal tubercles, and extensive webbing between the toes are present on the hind limbs. The diploid karyotype ($2n = 24$) includes three metacentric, seven submetacentric, one telocentric, and one subtelocentric chromosome pairs (Wiley 1982).

Tadpoles are 4.5–5.5 mm TL at hatching and grow to approximately 60 mm before metamorphosis, 28–44 days later. Ontogenetic color change is continuous until tadpoles reach Gosner (1960) stages 25 or 26, by which time light blotches fuse to form interorbital and transverse body bands. After this, the body is green, with a yellow to buff venter, a yellow tail with dark mottling or reticulations, and distinct yellow orbitonasal stripes. The yellow interorbital stripe sometimes is retained in large tadpoles, thus forming a triangle on the head. The tail is long. The dorsal tail fin originates on the back of the body, is arched, and its width is roughly equal to that of the ventral fin. Other external morphological characteristics include laterally bulging eyes, dextral anus, sinistral spiracle, and gap ratio between sections of the second anterior tooth row is three or greater.

• **DIAGNOSIS.** Several sympatric species of *Hyla* usually or occasionally are green and superficially resemble *H. cinerea*. Adult *H. cinerea* usually can be distinguished by the bold and

strongly bordered lateral stripes that the other species lack. Adult *H. squirella* are smaller (<41 mm TL), usually browner, but occasionally have light lateral stripes that are proportionally narrower than those of *H. cinerea*, and lack distinct lower borders. Adult *H. gratiosa* are larger (to 70 mm), of stouter proportions, and usually have dark-spotted and more granular dorsal skin. Adult *H. andersonii* are smaller (to 51 mm), have yellow to orange spots on the concealed surfaces of the thighs, and distinct brownish stripes that originate on the sides and run through the eyes. Individual *H. avivoca*, *H. chrysoscelis*, and *H. versicolor* often are green (although usually grading into gray on the sides), but usually have dark dorsal smudges and white or light gray squares below each eye. See also **Comments**.

• **DESCRIPTIONS.** Good descriptions of postmetamorphic individuals were provided in classic texts on North American anurans by Catesby (1754), Cope (1889), Dickerson (1906), LeConte (1825, 1855), Wright (1932), and Wright and Wright (1949), as well as in field guides, regional herpetofaunal guides, and keys by Ashton and Ashton (1988), Barbour (1971), Bartlett and Bartlett (1999), Behler and King (1979), Black and Sievert (1989), Brimley (1926, 1944), Cagle (1941, 1952), Chermock (1952), Conant and Collins (1998), Dixon (2000), Dundee and Rossman (1989), Dunn (1918), Forey and Fitzsimmons (1987), Garman (1892), Garrett and Barker (1987), Gibbons and Semlitsch (1991), Johnson (2000), Keiser and Wilson (1969), Lohoefer and Altig (1993), Martof et al. (1980), Mount (1975), Phillips et al. (1999), Powell et al. (1998), H.M. Smith (1978), and P.W. Smith (1961).

Descriptions of tadpole morphology or keys including tadpoles were provided by Altig (1970), Ashton and Ashton (1988), Brimley (1944), Cochran and Goin (1970), Dickerson (1906),

Morris (1944), Redmer et al. (1999), Travis (1981), and Wright (1929, 1932). The eggs were described by Cagle (1942), Garton and Brandon (1975), and Livezey and Wright (1947).

Breeding vocalizations, which consist of a series of nasal barks have been described variously as sounding like "frank frank frank..." or "quonk quonk quonk..." A number of quantified descriptions, sonograms, or audiospectrograms of the breeding vocalizations have been published (Allison 1992; Asquith et al. 1988; Blair 1958a,b; Bogert 1960; Ehret and Gerhardt 1980; Garton and Brandon 1975; Gerhardt 1974a,b,c, 1978a,b, 1981b, 1983, 1986; Gerhardt et al. 1980; Mudry and Capranica 1987; Oldham and Gerhardt 1975; Rigley and Hays 1976). Non-mating vocalizations have been described as well (Garton and Brandon 1975, Gerhardt 1978b, Rigley and Hays 1976).

• **ILLUSTRATIONS.** Color photographs are numerous in primary herpetological literature and in popular books and magazines. Some examples of color photographs of **adults** are in Ashton and Ashton (1988), Barbour (1971), Bartlett and Bartlett (1999), Behler and King (1979), Black and Sievert (1989), Brach (1998), Carmichael and Williams (1991), Conant and Collins (1998), Garrett and Barker (1987), Johnson (2000), Martof et al. (1980), Mattison (1993), Mitchell and Anderson (1994), Phillips et al. (1999), Redmer et al. (1999), and Rivero (1998). A color photograph of an amplexed pair is provided by Johnson (2000). Cain and Ustech (1976) show a color photograph of an aberrantly colored adult. Color illustrations of adults are in

Catesby (1754), Conant and Collins (1998), Dundee and Rossman (1989), and Smith (1978). Black and white photographs of adults are in Barbour (1971), Carr and Goin (1955), Dickerson (1906), Johnson (1977), Morris (1944), Mount (1975), Nietzke (1977), Smith (1961), Wright (1932), Wright and Wright (1949), and Yang et al. (1992). Black and white illustrations of **tadpoles** are available in Altig (1972), and Orton (1947). A color photograph of a tadpole is in Redmer et al. (1999). Black and white photographs of laboratory and natural **hybrids** between *H. cinerea* and other *Hyla* are in Anderson and Moler (1986), Kennedy (1964), and Mecham (1965), and color photographs by Fortman and Altig (1974). Black and white photographs of **habitats** are in Cagle (1942), Evers and Page (1977), Redmer et al. (1999), Smith (1961).

Miscellaneous illustrations include black and white photographs of dermal chromatophores (Bagnara et al. 1968; reproduced in Stebbins and Cohen 1995), marks caused by application of silver nitrate (Thomas 1975), skin sections of adults and tadpoles (Wygoda and Garman 1993), toe pads (Ernst 1973a, Linnenbach 1985), digital mucous glands (Ernst 1973b), tongue protrusion (Deban and Nishikawa 1992), drawings of the egg (Livezey and Wright 1947), ilial ontogenetic variation (Lynch 1966), karyotype (Wiley 1982), skin sections from adults (Elias and Shapiro 1957), skull (Gaudin 1974, Lamb and Avise 1987), spermatozoa (Delahoussaye 1966), and electromyograms of mating calls and laryngeal movements (Schmidt 1965). Good examples of commercially available audio recordings include Bogert (1958), Cornell Laboratory of Ornithology (1982), Elliot (1994), and Missouri Department of Conservation (1985).

• **DISTRIBUTION.** *Hyla cinerea* occurs primarily in swamps, sloughs, and weedy margins of lakes and ponds along the lower Atlantic and Gulf Coastal Plains, and the lower Mississippi River drainage of the southeastern United States (Conant and Collins 1998). The range extends southward from the Chesapeake Bay region of Delaware, Maryland, and Virginia through the Carolinas, Georgia, and Florida, then west through most of Alabama and Mississippi, all of Louisiana, the eastern half of Texas, and the Red River drainage of southeastern Oklahoma. In the Mississippi River drainage the range extends northward from Louisiana and Mississippi through the floodplains of southern and eastern Arkansas, western Tennessee and Kentucky, extreme southeastern Missouri, and southern Illinois. Introduced populations are reported from Puerto Rico (Hedges 1996, 1999; Powell et al. 1996; Rivero 1998; Schwartz and Thomas 1975; Schwartz and Henderson 1985, 1991), Brownsville, Texas (Conant 1977, Smith and Kohler 1977), central Missouri (Johnson 2000), and, perhaps, a coastal island in Florida (Smith et al. 1993). A population introduced to a fish farm in east central Kansas is probably extirpated (Collins 1993). Recent evidence of peripheral range expansion has been documented by Platt et al. (1999), Powell et al. (1995, 1996), Redmer et al. (1999), and Snyder and Platt (1997).

Maps of state-level or range-wide distributions were provided by Ashton and Ashton (1988), Barbour (1956), Bartlett and Bartlett (1999), Conant and Collins (1998), Dixon (2000), Garrett and Barker (1987), Dundee and Rossman (1989), Johnson (1977, 2000), Martof et al. (1980), Mitchell and Reay (1999), Mount (1975), Phillips et al. (1999), Redmer et al. (1999), Redmond and Scott (1996), Smith (1961), Tobey (1985), and Williams and Moulis (1994). Specific county or locality records and discussions of geographic distributions (by state) are as follows: **Alabama:** Petzing and Phillips (1998), Soehn et al. (1994); **Arkansas:** Black and Dellinger (1938), Dowling (1957), Irwin and Irwin (2002), Killebrew (1983), Parker (1947); **Delaware:** Conant (1958), Hardy (1972a), Reed (1956, 1960); **Florida:** Brimley (1910), Carr (1940), Carr and Goin (1955), Deckert

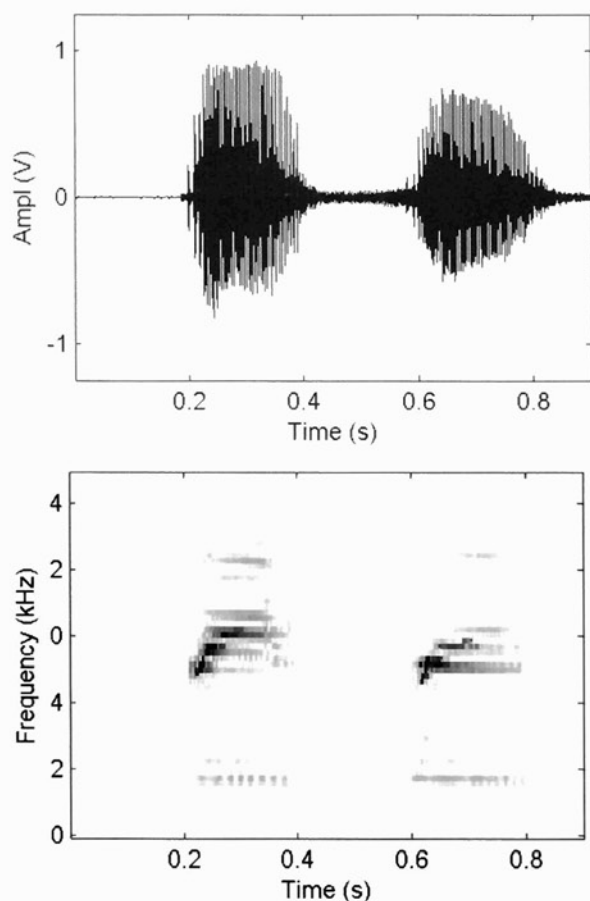


FIGURE 3. Ociologram (top) and audiospectrogram (produced with SoundRuler® software, Marcos Gridi-Papp, University of Texas at Austin) of two calling male *Hyla cinerea* in chorus, Leon County, Florida. Recorded 4 May 1988 by Lang Elliot. Digital calls (from CD track 15, Elliot 1994) used with permission of Lang Elliot, Nature Sound Studio (<http://www.naturesound.com>).

(1914), Duellman and Schwartz (1958), Iverson (1973), Peterson et al. (1952), Smith et al. (1993), Telford (1953), Van Hyning (1933); **Georgia**: Brandt (1953), Burt (1938), Laerm et al. (1999), Martof (1956, 1963), Neill (1949), Wharton and Howard (1971), Williams and Moulis (1994); **Illinois**: Cagle (1942), Davis and Rice (1883a,b), Evers and Page (1977), Garman (1890, 1892), Hurter (1893 [record discounted by Redmer et al. 1999]), Klimstra and Hutchinson (1965), Redmer and Ballard (1995), Redmer et al. (1999), Rossman (1960), Smith (1961); **Kentucky**: Barbour (1956, 1971), Drury and Gessing (1940), Lodato and Grannan (1990), Scott and Koons (1993a); **Louisiana**: Anderson et al. (1952), Boundy (1998), Burt and Burt (1929), Greenbaum (1998), Hardy (1995), Liner (1954, 1955, 1997), Walker (1963); **Maryland**: Conant (1958), Cooper (1950, 1956), Hardy (1972a), Noble and Hassler (1936), Reed (1956, 1957b, 1960); **Mississippi**: Allen (1932), Brimley (1910), Burt (1938); **Missouri**: Hurter (1911), Lowery (1951), Powell et al. (1995, 1996); **North Carolina**: Beane (1989, 1990), Brimley (1944), Burt (1938), Funderburg (1955), Gosner and Black (1956), Myers (1924); **Oklahoma**: Bragg (1952), Taylor and Laughlin (1964), **South Carolina**: Burt (1938), Gibbons and Harrison (1981), Gibbons and Semlitsch (1991), Jobson (1940), Obrecht (1946), Phelps and Lancia (1995), Snyder and Platt (1997); **Tennessee**: Blanchard (1922), Burt (1938), Gentry (1955), Peterson and Wirwa (1997), Rhoads (1895), Scott and Koons (1993b), Scott and Snyder (1967), Scott et al. (2000), Smith and Therrell (1999); **Texas**: Blair et al. (1995), Brown (1950), Burger et al. (1949), Cobb and Cobb (1991), Hallowell (1856), Hardy (1995), Hibbitts and Malone (1999), Irwin and Collins (1996), Karges (1979), McCoid (1998), McCord (1993), Merkord (1975), Olson (1967), Peterson (1950), Pope (1919), Rakowicz et al. (1983), Raun (1959), Raun and Gehlbach (1972), Roberts and Shilling (1991), Smith and Sanders (1952), Strecker (1902, 1908a, b, c, 1909, 1926a, b, 1930, 1935), Strecker and Johnson (1935), Strecker and Williams (1927), Tanzer et al. (1966), Vance (1980), Whiting and Price (1994), Wright and Wright (1938); **Virginia**: Conant (1958), Hardy (1972a), Mitchell and Anderson (1994), Reed (1956, 1957a, c, 1960), Richmond and Goin (1938), Tobey (1985), Werler and McCallion (1951). Occurrence in southeastern United States **National Forests** was listed by Seehorn (1982). **Biogeography** was discussed by Blair (1949), Brodman (1998), Duellman and Sweet (1999), Dowling (1956), Goin (1958), Lohoefer and Altig (1993), Lowery (1951), Owen (1989), Owen and Dixon (1989), Redmer et al. (1999), Smith and Buechner (1947), Smith and Minton (1957), and Smith (1961).

• **FOSSIL RECORD.** Recent material has been used for comparative purposes in studies of fossil hylid frogs (see **Pertinent Literature**), but only one fossil of *H. cinerea* is reported, from the Pleistocene (Kansan or Illinoian) of Alachua County, Florida (Lynch 1966). Several fossils identified as *Hyla* cf. *cinerea* have been reported from the Pliocene of Trego County, Kansas (Holman 1975, 1981) and Brown and Keya Paha counties, Nebraska (Chantell 1964, 1971; Estes and Tihen 1964; Holman 1976).

• **PERTINENT LITERATURE.** Probably because *Hyla cinerea* is widely distributed, generally abundant, and attractive, it is popular both as a terrarium pet and as a research organism. The literature on this species is extensive. Many popular references were very general and are not included.

Studies of geographic variation and/or relationships with other Holarctic hylids have addressed **breeding calls and other isolating mechanisms** (Asquith et al. 1988; Blair 1941; Blair 1958a,b,c, 1959; Gerhardt 1974b, 1981b; Lamb 1987; Oldham and Gerhardt 1975; Rigley and Hays 1976), **cladistic analysis**

(Cocroft 1994), **fitness and genetic heterozygosity** (McAlpine 1993, McAlpine and Smith 1995), **hybridization** (Anderson and Moler 1986; Blair 1958a; Fortman and Altig 1974; Gerhardt 1974b; Kennedy 1964; Lamb 1987; Lamb and Avise 1986, 1987; Lamb et al. 1990; Lee 1968; Littlejohn 1961; Mable and Rye 1992; Maxon et al. 1987; Mecham 1960, 1961, 1965; Pierce 1975; Pyburn and Kennedy 1961; Ralin 1977; Schlefer et al. 1986), **immunodistance** (Maxon 1978, Maxon and Wilson 1975, Maxon et al. 1987), **karyotype** (Anderson 1991, Anderson and Moler 1986, Bachmann et al. 1966, Becak et al. 1973, Bushnell et al. 1939, Wiley 1982), **lateral stripe polymorphism** (Aresco 1996; Conant 1958; Dunn 1918, 1937; Smith 1961; Reed 1956; Wright and Wright 1949; see also **Nomenclatural History**), **morphology** (Aresco 1996, Glass 1946, Jameson and Richmond 1971, Mount 1975, Smith 1961), **mtDNA polymorphism** (Bermingham et al. 1986), **osteology** (Gaudin 1974), **osteology of recent compared with fossil hylids** (Chantell 1964, 1971; Holman 1961, 1962, 1963, 1967, 1968, 1969, 1975, 1976, 1981), and **protein comparisons** (Dessauer et al. 1957, Guttman 1973, Hedges 1986, Highton 1991, Karlin et al. 1982).

Papers on gross anatomy and morphology are: **biomechanics** (Deban and Nishikawa 1992, Martin 1972, Zug 1985), **ontogenetic change** (Blouin 1991, 1992a,b; Blouin and Loeb 1991), **optic nerve** (Maturana 1959, 1960), **pectoral girdle** (Martin 1972), **pigmentation** (Bagnara and Obika 1965, Bagnara et al. 1968, Nielsen 1978, Nielsen and Dyck 1978, Taylor 1969), **skin histology** (Elias and Shapiro 1957), **spermatozoa** (Delahoussaye 1966), **toe pads and their mucous glands** (Ernst 1973a,b), and **tooth development** (Goin and Hester 1961).

Ecological papers have addressed **anuran associates** (Brown and Pierce 1965, Cagle 1942, Garton and Brandon 1975, Eason and Fauth 2001, Given 1999, Grimké and Jaeger 1998, Hardy 1972a, Livezey and Johnson 1948, Merovich and Howard 2000, Moore 1976, Peterson et al. 1952, Redmer et al. 1999, Trauth 1992, Wright 1932, Wright and Wright 1949), **occurrence in brackish water or coastal waterways** (Allen 1932, Conant 1958, Diener 1965, Dunn 1937, Martof 1963, Mitchell and Anderson 1994, Moore 1976, Mueller 1985, Neill 1958, Oliver 1955, Smith et al. 1993), **chorus size** (Bancroft et al. 1983), **climbing and perch height** (Cloudsley-Thompson 1999), **commensal/symbiotic organisms** (Harman and Lawler 1975, Parish 1998, Yang and TeBeest 1992, Yang et al. 1992), **defense mechanisms** (Blouin 1990, Marchison and Anderson 1978, Richardson 2002b), **demography** (O.B. Goin 1958), **density and age of a tadpole cohort** (Turnipseed and Altig 1975), **development and ontogeny** (Altig 1972; Bagnara and Obika 1965; Bagnara et al. 1968; Ballinger and McKinney 1966; Blouin 1991a,b; Blouin and Loeb 1991; Cagle 1942; Garton and Brandon 1975; Guttman 1973; Orton 1947; Taylor 1969; Turnipseed and Altig 1975; Will 1988; Wright and Wright 1949), **diet** (Brown 1974, Freed 1982a, Haber 1926, Kilby 1945, Oliver 1955, Ritchie 1982), **dispersal of juveniles** (Bartsch 1944, Garton and Brandon 1975, Redmer et al. 1999), **fecundity** (Garton and Brandon 1975, Perrill and Daniel 1983, Trauth et al. 1990), **growth** (Blouin 1991, 1992a,b; Garton and Brandon 1975), **habitat** (Anderson et al. 1952; Andrews 1928; Bartsch 1944; Brown 1974; Burbrink et al. 1998; Cagle 1942; Carr 1940; Carr and Goin 1955; Dundee and Rossman 1989; Eason and Fauth 2001; Funderburg 1955; Garton and Brandon 1975; Goin 1943; Hurter 1911; Lee 1969; Jobson 1940; LeConte 1825; Merovich and Howard 2000; Metts et al. 2001; Mierzwa 1998; Mitchell and Miller 1991; Mount 1975; Neill 1951; Redmer et al. 1999; Rossman 1960; Scott and Koons 1993a,b; Smith 1961; Tinkle 1959; Turnipseed and Altig 1975; Werler and McCallion 1951; Wright 1932), **interspecific interactions of tadpoles** (Grimké and Jaeger 1998), **mortality** (Tinkle 1959), **mortality and recruitment of tadpoles** (Roth and Jackson 1987), **ovipos-**

sition sites (Garton and Brandon 1975, Mount 1975, Turnipseed and Altig 1975), **parasites** (Brooks 1979, Creel et al. 2000, Harwood 1933, Johnson et al. 1993, McKeever 1977, Nelson et al. 2002, Okafor et al. 1984, Steiner 1924), **predators** (Bishop and Farrell 1994, Bowers 1966, Garton and Brandon 1975, Jenni, 1969, Lockley 1990, Mitchell 1994, Palmer and Braswell 1995, Schardien and Jackson 1982, Wright 1932, Wright and Wright 1949), **pre-hibernation weight** (McCallum and Trauth 2001), and **refugia or hibernacula** (Andrews 1928, Boughton et al. 2000, Delnicki and Bolen 1977, Garton and Brandon 1975, O.B. Goin 1958, McAllister et al. 1995, McComb and Noble 1981, Tinkle 1959).

Warm air temperatures ($>20^{\circ}\text{C}$) may be more important in initiating chorusing than is precipitation (Dundee and Rossman 1989, Garton and Brandon 1975, Mount 1975, Wright 1932). The chorusing and breeding season is longest in the south (March to October), and much shorter (May to August) in the extreme northern part of the range. Specific **chorus dates or breeding seasons** have been reported for **Alabama** (Mount 1975), **Florida** (Ashton and Ashton 1988, Bancroft et al. 1983, Einer and Ober 1956, Moulton 1954, Wright and Wright 1949), **Georgia** (Wharton and Howard 1971, Wright 1932), **Illinois** (Brown and Pierce 1965, Garton and Brandon 1975, Redmer et al. 1999, Smith 1961), **Kentucky** (Scott and Koons 1993), **Louisiana** (Dundee and Rossman 1989), **Missouri** (Johnson 2000), **North Carolina** (Beane 1990), **South Carolina** (Gibbons and Harrison 1981, Jobson 1940, Mohr and Dorcas 1999), **Tennessee** (Gentry 1955), **Texas** (Garrett and Barker 1987, Pope 1919), and **Virginia** (Werler and McCallion 1951).

Literature on other aspects of reproductive behavior and ecology includes **chorus tenure of males** (Gerhardt et al. 1987), **mate choice** (Asquith and Altig 1990; Gerhardt 1978b, 1982, 1986, 1991; Gerhardt and Klump 1988, 1991; Klump and Gerhardt 1986, Wells 1977), **male combat** (Garton and Brandon 1975), **mating strategies** (Garton and Brandon 1975; Goin and Goin 1953; Mitchell and Miller 1991; Perril 1984; Perril et al. 1978, 1982; Wells 1977; Wright 1932), and **mating success** (Gerhardt et al. 1987).

Papers on non-reproductive behaviors have addressed **activity and predator avoidance** (Richardson 2001, 2002b), **ecdysis** (Oliver 1955), **feeding behavior/strategy** (Deban and Nishikawa 1992; Freed 1980a,b, 1982a,b, 1988; Huheey 1980), **food availability and tapoles** (Leips and Travis 1994), **homing ability** (O.B. Goin 1958), **locomotion** (Janson 1953, Marsh and John-Alder 1994, Zug 1985), and **sleep behavior** (Hobson et al. 1967, 1968).

Papers on thermal ecology and water balance have addressed **advantages of thermoregulation** (Freed 1980b, O.B. Goin 1958), **body temperatures** (Brattstrom 1963, 1968, 1970), **cooling** (Wygoda 1988b), **factors affecting evaporative water loss** (Wygoda 1984, 1988a,b, 1989a,b; Wygoda and Garman 1993, Wygoda and Williams 1991), **fever** (Kluger 1977, Muchlinski 1985), **effects of low pH** on tadpole swimming performance (Jung and Jagoe 1995), **pond hydroperiod and larval phenotypic plasticity** (Leips et al. 2000, Richardson 2002a), **thermal acclimation/tolerances** (Ballinger and McKinney 1966, Blem et al. 1986, Brattstrom 1963, Layne and Romano 1985, Layne et al. 1985), **tolerance of desiccation by *H. cinerea* and hybrids** (Layne et al. 1989), and **water absorption** (Walker and Whitford 1971).

Populations appear to be secure throughout the species' range, although actual studies have been few. General comments on **abundance or reviews of conservation status** in individual states have been made by Ackerman (1975), Anderson et al. (1952), Ashton (1976), Ashton and Ashton (1988), Bancroft et al. (1983), Bartlett and Bartlett (1999), Bider (1962), Dundee and Rossman (1989), Dyrkacz (1974), Gibbons (1983), Gib-

bons and Semlitsch (1991), O.B. Goin (1958), Hanlin et al. (2000), Johnson (2000), Lannoo (1998), LeConte (1825), Liner (1954, 1955b), Mount (1975), Platt et al. (1999), Phillips et al. (1999), Redmer et al. (1999), and Smith (1961). Two reports of apparent localized **population decline** are Delis et al. (1996) and Dodd and Griffey (2002).

Human activities that may effect habitat, individuals, and populations include **range expansion mediated by creation of artificial lakes and ponds** (Platt et al. 1999, Redmer et al. 1999), **environmental toxicity** (Dapson and Kaplan 1975, Jung and Jagoe 1995, Mahaney 1994, Webber and Cochran 1984), **fish introductions** (Bancroft et al. 1983, McDiarmid et al. 1983, Redmer et al. 1999), **fire** (Babbitt and Babbitt 1951, Komarek 1969), **hybridization following habitat disturbance** (Mecham 1960, Schlefer et al. 1986), **suggestions for habitat management** (Wilson, 1995), **effects of highway traffic noise on reproductive behavior** (Barrass 1986), **introduction/translocations** (Meshaka 1996, Redmer et al. 1999), **silver nitrate used to mark individuals** (Thomas 1975), **timber harvest** (Hanlin et al. 2000, Phelps and Lancia 1995), and **trapping success** (Boughton et al. 2000, Campbell and Christman 1982, Gibbons and Semlitsch 1981, Moulton et al. 1997). The introduction and spread of the **Cuban Treefrog** (*Osteopilus septentrionalis*) in southern Florida may negatively impact the smaller species of *Hyla* (including *H. cinerea*) upon which it preys and with which it may compete, although no empirical data support this belief (Wilson and Porras 1983).

Articles addressing **captive husbandry** are abundant in the popular literature and a few journals. Some of these are Brach (1998), Edmonds (1992), Fredricksen (1977), Greckhamer (1992a,b), Heselhaus (1987), Mattison (1993), and Nietzsche (1977). Specialized topics include **captive longevity** (Slavens and Slavens 1993), **captive reproduction** (Vleminkcz 1988), and **veterinary treatment** (Brown 1995, limb amputation and rehabilitation).

Studies of endocrinology include **effects of corticosterone on behavior** (Burmeister et al. 2001), **effects of vasotocin on behavior** (Burmeister et al. 2001), **effects of melatonin on gonosomatic index** (DeVlaming et al. 1974), **melanophorotropic potency of ACTH** (Edgren 1954), **factors affecting color change** (Ferguson 1948, Nielson 1978, Nielsen and Dyck 1978, Taylor 1969), **hormonal response to social stimuli** (Burmeister and Wilczynski 2000, 2001), **response to human chorionic gonadotropin** (Knepton 1951), and **reflectance response to melanophore hormone** (Teague and Patton 1960a,b, 1963).

Hyla cinerea has been used extensively as a model for integrated studies in auditory, behavioral, and neural physiology including **behavioral and neural responses to breeding calls** (Allison 1992; Allison and Wilczynski 1991, 1994; Blair 1958d; Bogert 1960; Capranica 1992; Feng, 1975; Feng and Capranica 1978; Feng et al. 1976; Gerhardt 1974a,c, 1978a,b, 1981a, 1982, 1983, 1986, 1987, 1991; Gerhardt et al. 1990; Gerhardt and Mudry 1980; Megela and Capranica 1981; Megela-Simmons 1988; Mudry and Capranica 1987; Rheinlaender and Klump 1988; Rigley and Hays 1976; Schmidt 1966a, 1969, 1971), **effects of body size on response to sound** (Hetherington 1992, 1994), **calling evoked by airplane sounds** (Fowler 1960), **effect of breathing on auditory physiology** (Ehret et al. 1994, Schmidt 1966a), **energetic costs of chorusing** (Prestwich et al. 1989), **frequency selectivity** (Moss and Megela-Simmons 1986), **hormonal effects on calling and auditory sensitivity** (Penna and Capranica 1984; Penna et al. 1992; Schmidt 1966a,b), **laryngeal mechanics of call production** (Schmidt 1965), **long-range communication** (Littlejohn 1977), **middle-ear structure and function** (Hetherington 1992, 1994; Jaslow et al. 1988; Moffat and Capranica 1978), **neuroanatomy** (Wilczynski and Zakon 1982), **neurophysiology** (Lim and Capranica 1994,

Marrero et al. 1991, Sutherland and Nennemacher 1981, Zakon and Wilczynski 1988), **effects of noise on mate choice** (Gerhardt and Klump 1988, 1991; Klump and Gerhardt 1986), **olfactory neurology** (Meyer et al. 1995), **otoacoustic emissions** (van Dijk et al. 1996), **otoacoustic inhibition** (van Dijk et al. 2001), **perception of complex sounds** (Simmons et al. 1993), **phonotaxis** (Feng 1975; Feng and Capranica 1978; Gerhardt and Rheinlaender 1982; Michelson et al. 1986; Rheinlaender 1978; Rheinlaender and Klump 1988; Rheinlaender et al. 1979, 1981; Schwartz and Gerhardt 1989), **properties of breeding calls** (Allan and Magela-Simmons 1994, Asquith et al. 1988, Ehret and Gerhardt 1980, Oldham and Gerhardt 1975, Rigley and Hays 1976), and **tone suppression in auditory nerves** (Ehret et al. 1983).

• **ETYMOLOGY.** The specific epithet is based on the Latin stem *ciner-* (ashes or ashen), and probably refers to the gray or brown coloration of preserved specimens.

• **NOMENCLATURE HISTORY.** In the 1800s, the name *Calamita carolinensis* was repeatedly and erroneously used as an older name attributed to Pennant (1792). Further discussion of this usage is in Rhoads (1895), Duellman and Schwartz (1958), and Frost (2000).

From the late 1800s through the mid-1900s, most taxonomic discussions of *H. cinerea* have been based on variation in, or lack of, the light lateral stripe. Specimens with lateral stripes reduced in length were referred to as *H. semifasciata* Hallowell 1857. *Hyla semifasciata* was synonymized by Boulenger (1882), but was treated as a subspecies of *H. cinerea* by Rhoads (1895). In some populations in the Chesapeake Bay region of Delaware, Maryland, and Virginia, most individuals lack lateral stripes and were described as *Hyla evittata* by Miller (1899), which Dunn (1918, 1937) treated as *H. c. evittata*. For approximately sixty years, most authors used the trinomial and referred to intergrades between *H. c. cinerea* and *H. c. evittata* (Barbour 1956; Bartsch 1944; Brandt 1953; Brimley 1926, 1944; Burt and Burt 1929; Carr and Goin 1955; Conant 1958; Cooper 1950; Diener 1965; Dunn 1918, 1937; Einer and Ober 1956; Gentry 1955). Reed (1956) argued against the usage of *H. c. evittata*, and with few exceptions the name *H. evittata* has since been considered a synonym of *H. cinerea*. Neither Crother (2000) nor Collins and Taggart (2002) recognized the subspecies; the former explicitly rejected their use.

• **COMMENTS.** Individuals of several sympatric species of *Hyla* sometimes superficially resemble *H. cinerea*. Resemblance is perhaps greatest in the smaller *H. squirella*, and the two species often are collected together. In some museum collections, we found significant numbers (as many as 17%) of specimens of these species misidentified. Other museum specimens misidentified as *H. cinerea* include individuals of *H. femoralis*, *H. chrysoscelis*/*H. versicolor* complex, and *H. gratiosa*. A field guide account has a color photograph of an adult *H. squirella* misidentified as *H. cinerea* (Behler 1988). *Hyla flavivulva* Glass 1946 was based primarily on misidentified specimens (which we have examined) of *Hyla squirella* (Wright and Wright 1949, Martof 1975), but which were originally compared by Glass (1946) to *H. cinerea*.

Hyla cinerea has been granted symbolic status as the official amphibian of the Commonwealth of Louisiana. A similar measure was proposed by the State of Georgia, but as of this writing has not been adopted.

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